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# BIOLOGY AND IMMATURE STAGES OF CHLOROPIDAE (INSECTA: DIPTERA) ASSOCIATED WITH SPIKE-RUSHES (CYPERACEAE: *ELEOCHARIS*) I. STEM BORERS

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## ABSTRACT

The life cycles and larval feeding habits of one species of *Chlorops* (*C. obscuricornis* Loew) and three species of *Diplotoxa* [*D. inclinata* Becker, *D. nigripes* (Coquillett), and *D.* sp. near *versicolor* (Loew)] associated with spike-rushes of the genus *Eleocharis* (Cyperaceae) are presented. Larvae of the four species show resource partitioning by attacking either stems or rhizomes, by feeding at different times, or by utilizing different species of *Eleocharis.*

This study compares the morphology of the larvae; describes and illustrates the eggs, three larval instars, and puparia of three species of *Diplotoxa*; and provides a key separating the third-instar larvae of all four species of *Eleocharis* stem borers.

## INTRODUCTION

The sedge genus *Eleocharis,* containing about 150 species in the world, is nearly cosmopolitan in distribution and is particularly well-represented in warmer regions. It is easily distinguished from other genera of Cyperaceae by the presence of a single, terminal, spike-like inflorescence that lacks obvious subtending bracts. Both annual and perennial species occur. Determining species is difficult, as well-developed seed heads and achenes are necessary for identification (Gleason, 1963; Braun, 1967; Scoggan, 1978). Species of *Eleocharis* frequently form nearly pure stands in open wetlands, perhaps due to their ability to secrete compounds that inhibit the growth of other hydrophytic plants (Wooten and Elakovich, 1991).

The importance of spike-rushes to chloropid flies was indicated by Todd and Foote (1987) who reported that a stand of *E. smallii* Britton contained ten of the 22 species of Chloropidae collected in eight vegetation types occurring in a freshwater marsh near Kent, Ohio.

*Chlorops,* a member of the subfamily Chloropinae, is the largest chloropid genus in North America, containing 35 species (Sabrosky, 1987). Most of the available information on the biology of the genus is based on studies of the gout fly, *C. pumilionis* Bjerkander (*C. taeniopus* Meigen, *auct.*), an economically important pest of cereal grains in Europe. The stem-boring larvae of that species were described in detail by Frew (1923*a,* 1923*b*), Balachowsky and Mesnil (1935), Goodliffe (1939, 1942), Nye (1958), and Dennis (1961). Other European species that are stem borers of grasses are *C. speciosa* Meigen, *C. brevimana* Loew, *C. interrupta* Meigen, and *C. marchali* Mesnil (Ferrar, 1987). A few species of Nearctic *Chlorops* have larvae that are primary invaders of sedge stems (Valley et al., 1969). Recently,

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Rogers et al. (1991) elucidated the life history and described the immature stages of *C. certimus* Adams, a species whose larvae attack stems of the sedge genus *Carex.*

*Diplotoxa,* also a member of the subfamily Chloropinae, is a cosmopolitan genus that has been recorded in nearly all the biogeographic regions. Five of the seven Nearctic species, *D. alternata* (Loew), *D. inclinata* Becker, *D. messoria* (Fallén), *D. recurva* (Adams), and *D, versicolor* (Loew), are practically transcontinental in distribution; *D. unicolor* Becker is restricted to the western states and provinces; and *D. nigripes* (Coquillett) occurs only in the eastern and midwestern states and provinces (Sabrosky, 1965).

Few papers have been published on the larval feeding habits and host plants of *Diplotoxa.* Wendt (1968) reported that larvae of *D. messoria* are phytophagous in European species of *Eleocharis,* but gave no information concerning host plant specificity, larval feeding habits, or life cycle parameters. Valley et al. (1969) reared *D. messoria, D. nigripes,* and *D.* sp. (near *D. inclinata*) from stems of *Eleocharis* in North America. Spencer (1977) reared a New Zealand species from inflorescences of a grass of the genus *Echinochloa.* No immature stage of any species has been described (Ferrar, 1987).

The present paper elucidates the life cycles and larval feeding habits of one species of *Chlorops* and three of *Diplotoxa* that attack the stems and rhizomes of *Eleocharis* spp. in northeastern Ohio. The immature stages of three species of *Diplotoxa* are described and illustrated, and a key is given to the third instars of all four species of *Eleocharis* stem borers. In addition, certain morphological structures found in the larvae are compared.

## Materials and Methods

*Collecting Techniques.*—Adults were collected weekly by sweeping vegetation of suitable habitats with a standard aerial insect net. Collecting sites were all located in Portage County in northeastern Ohio. Eggs were collected in nature by pulling up *Eleocharis* plants in the field and examining them in the laboratory. Larvae and puparia were found during the winter and spring by examining developing rhizomes, the bases of young shoots, and new stems of *Eleocharis* that were approximately 0.5–1.0 in in height.

*Rearing Techniques.*—Adult flies were sexed and paired, and placed in baby food jars (9 × 6 cm) which had their bottoms removed. The jars were inverted, and the top pressed into the bottom of a small plastic Petri dish (5.5 × 1.3 cm) containing moist peat moss. The open bottom of the jar was covered with 1–4 layers of cheesecloth held in place by a rubber band. A small pellet of honey and brewer's yeast pressed to the side of the jar served as adult food. The peat moss was moistened daily, and the fly food replaced periodically. Small sections of *Eleocharis* stem, approximately 5–6 cm in length, were oriented vertically in the peat moss to provide oviposition sites. These were replaced periodically with fresh sections, as females would not oviposit on decomposed material.

Eggs removed from the rearing jars were placed in small Petri dishes (5.4 × 1.3 cm) containing discs of moist paper toweling; occasionally whole stem sections containing eggs were transferred.

Newly-hatched larvae were placed on young shoots of *Eleocharis* and examined daily for information on larval feeding habits, length of larval stadia, and sites of pupation. Larvae were transferred to fresh plant material regularly, as they quickly abandoned decaying stems. Puparia were transferred to small Petri dishes containing moist peat moss. Parasitoid wasps emerging from puparia were killed and preserved in 70% ETOH.

*Preservation and Preparation of Specimens.*—Approximately 10–20 eggs of each species were measured and preserved in KAAD. Larvae were killed in hot (not boiling) water and were either preserved in 70% alcohol or treated for further study, and drawn using standard light microscopy techniques.

Abbreviations used in figures are: A, antenna; AP, anterior papilla; APB, anterior end of parastomal bar; ApT, apical tooth; ASL, anal slit; ASp, anterior spiracle; AT, accessory tooth; Cph, cephalopharyngeal skeleton; DC, dorsal cornu; FP, frontal papilla; GP, genal papilla; HS, hypopharyngeal sclerite; IP, interspiracular process; LP, lateral papilla; LS, ligulate sclerite; m, membrane; MH, mouthhooks; MP, maxillary palp; Pa, papilla; PB, parastomal bar; PcS, pseudocephalic segment; PfP, pre-

frontal papilla; PhS, tentoropharyngeal sclerite; PP, perianal pad; PSP, posterior spiracular plate; R, ramus; SB, spinule band; ShS, subhypopharyngeal sclerite; SSl, spiracular slit; StB, stigmatic bulb; StSc, spiracular scar; StT, stigmatic tube; Tr, trabecula; TP, thoracic papilla; VC, ventral cornu; WP, wing process of hypostomal sclerite.

## LIFE HISTORIES

### *Chlorops obscuricornis* Loew

This species is strictly Nearctic in distribution, ranging from Virginia and New York west to Manitoba and Oregon and south to Florida and California (Sabrosky, 1965). Valley et al. (1969) reported that the larvae were primary invaders of stems of *Eleocharis smallii.*

Rearings were initiated from numerous adults and immature stages collected from stands of *E. smallii,* a perennial species having sizeable reddish or purplish rhizomes. The fidelity of *C. obscuricornis* to its host plant was shown by Todd and Foote (1987) who found adults almost exclusively in a stand of *E. smallii.* At another marsh, a few adults were swept from a stand of *E. obtusa* (Willd.) Schultes, an annual species. Numerous adults were also swept from another perennial species, *E. rostellata* Torrey, in a calcareous fen. The flight period, as determined by weekly sweep samples of a stand of *E. smallii* occurring in a roadside ditch, lasted from early June to mid-July (Fig. 54). Adults were most abundant in mid-June.

Laboratory-reared females lived 12–19 days ($n = 8$); males, 8–11 days ($n = 8$). No courtship displays were noted, and it appeared that males merely assaulted any nearby fly of proper size and configuration. Nonreceptive females dislodged males by vigorous kicking of their hind legs. During copulation the male situated himself above the female, facing in the same direction. The fore tarsi rested on the bases of her folded wings, his middle tarsi were applied to the lateral surface of her abdomen, and the hind tarsi grasped the female's genitalic segments.

Both field-collected and reared females laid eggs readily on lengths of *Eleocharis* stems in the breeding jars. All field-collected eggs were found near the bases of stems. The incubation period lasted 5–7 days ($n = 12$). No larvae were reared to the pupal stage in the laboratory-initiated rearings. Second-instar larvae were found during late March feeding as primary invaders in stems of *E. smallii.* A few larvae occurred in young shoots, but most were in larger, older stems. Fully grown larvae were found by the middle of April. Shortly before forming puparia, larvae retreated to the crown, tunneled into one of the rhizomes, reversed direction, and inserted their posterior spiracles into the hollowed-out portion of the rhizome. Field-collected puparia produced adults in 10–15 days under laboratory conditions ($n = 4$).

The abbreviated flight period (Fig. 54) suggests that *C. obscuricornis* is univoltine in northern Ohio. Overwintering apparently occurred as young larvae in quiescence. Larvae collected during the winter months became active in the laboratory and began feeding on *Eleocharis* stem tissue. Larval feeding was completed in nature in April and early May, pupation occurred in late May, and adults emerged in June. Eggs were deposited between mid-June and early July. Larvae fed in the stems until late October.

### *Diplotoxa inclinata* Becker

*Diplotoxa inclinata* has a transcontinental distribution, ranging from Québec to California and south to New Jersey and Texas (Sabrosky, 1965). It was abundant

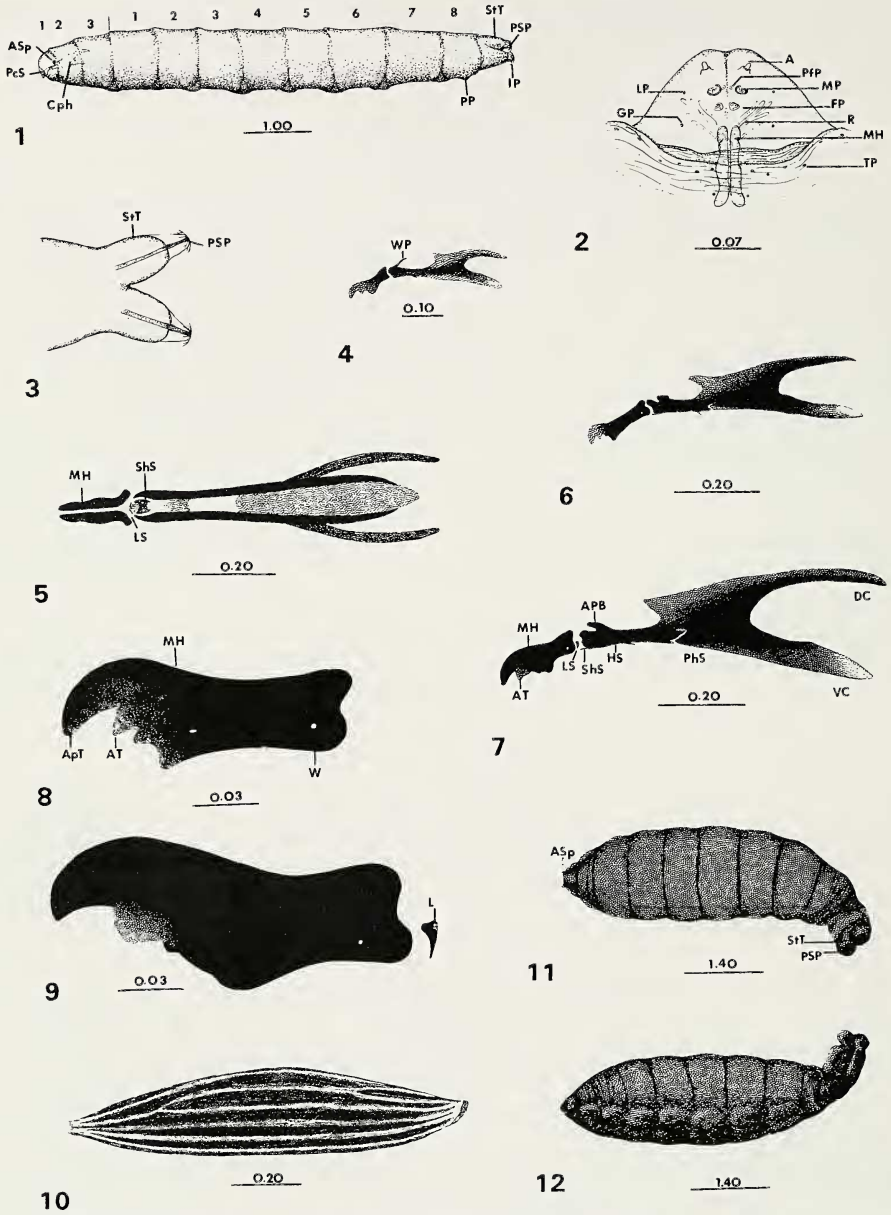


Fig. 1–12.—*Diplotoxa nigripes.* 1. Lateral habitus of larva, third instar. 2. Ventral view of anterior end, same. 3. Dorsal view of posterior end, same. 4. Lateral view of cephalopharyngeal skeleton, first instar. 5. Ventral view of cephalopharyngeal skeleton, third instar. 6. Lateral view of cephalopharyngeal skeleton, second instar. 7. Same, third instar. 8. Mandible, second instar. 9. Same, third instar. 10. Egg. 11. Puparium, dorsal view. 12. Same, lateral view.

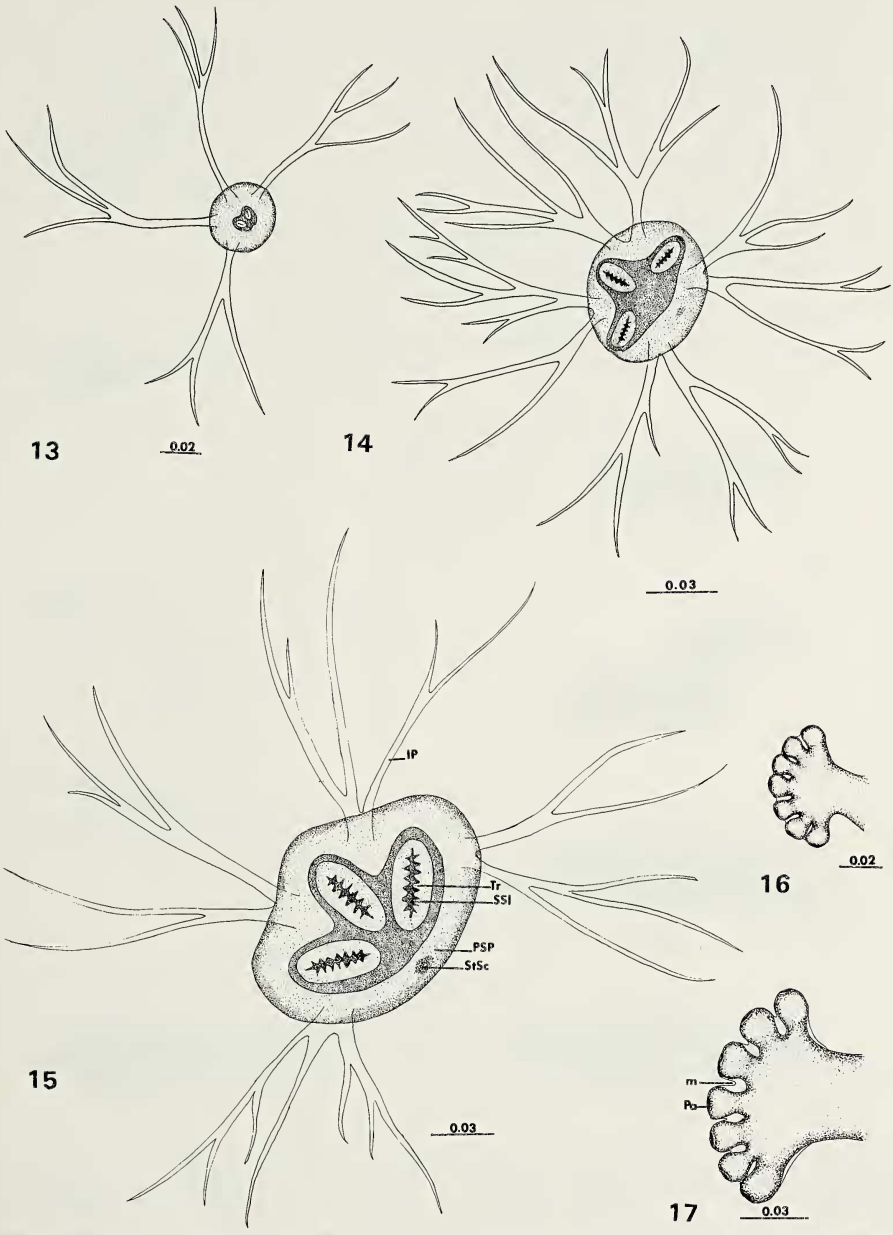


Fig. 13–17.—*Diplotoxa nigripes.* 13. Posterior spiracular plate, first instar. 14. Same, second instar. 15. Same, third instar. 16. Anterior spiracle, second instar. 17. Same, third instar.

in freshwater marshes in northeastern Ohio that contained stands of its host plant, *Eleocharis smallii* (Todd and Foote, 1987). Several adults were also swept from a small stand of *E. obtusa.* This was one of the first species of *Diplotoxa* to emerge in the Kent area, as six adults were collected as early as May 5. The flight period lasted from early May until early September (Fig. 55). Weekly sweep samples of adults strongly suggest that there are two generations a year in northeastern Ohio.

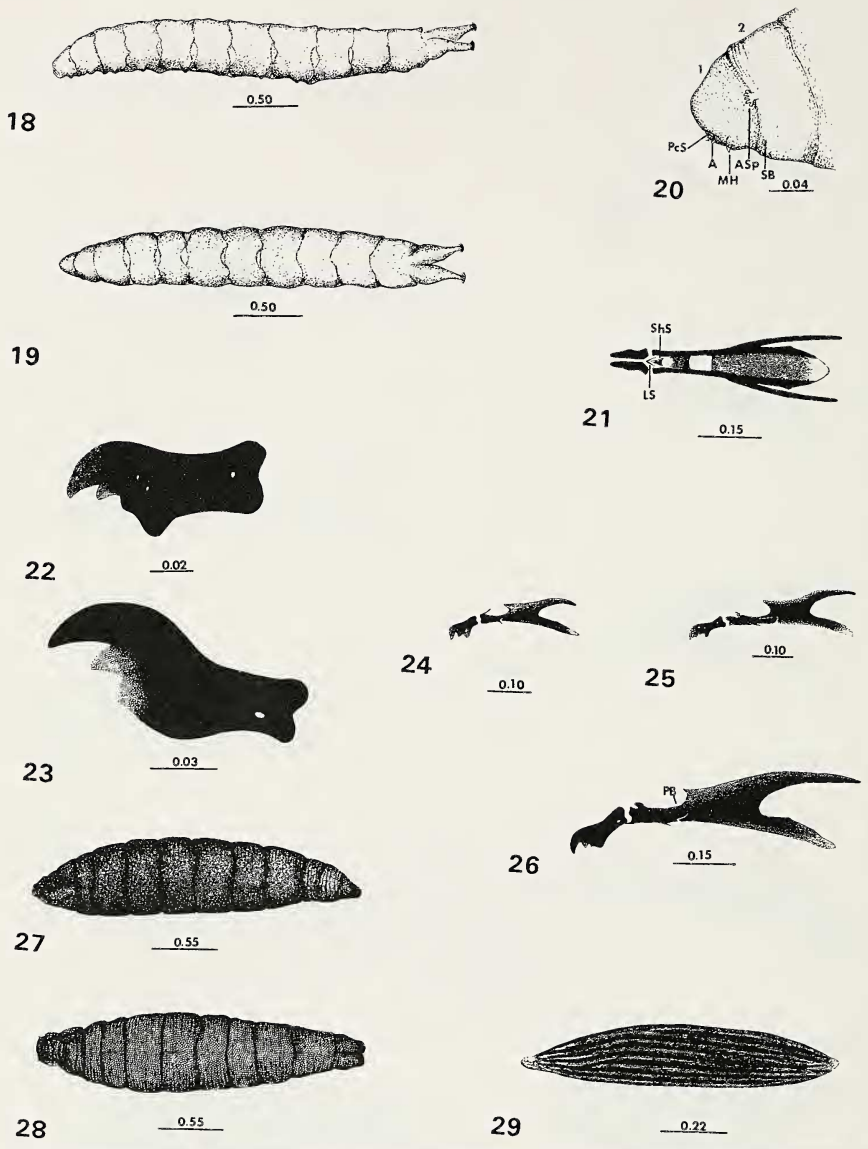


Fig. 18–29.—*Diplotoxa* sp. near *versicolor*. 18. Lateral habitus, third instar. 19. Dorsal habitus, same. 20. Lateral view of segment 1, third instar. 21. Ventral view of cephalopharyngeal skeleton, third instar. 22. Mandible, second instar. 23. Same, third instar. 24. Lateral view of cephalopharyngeal skeleton, first instar. 25. Same, second instar. 26. Same, third instar. 27. Puparium, lateral view. 28. Same, dorsal view. 29. Egg.

Adults usually rested head downward on *Eleocharis* stems. Paired adults placed in breeding jars with lengths of *Eleocharis* spent most of their time on the stems and did not wander freely about the enclosure. Field-collected females lived 7–21 days in the laboratory ($n = 10$); males, 12–17 days ($n = 10$). In contrast, reared females lived only 4–18 days ($n = 5$). Reared females usually had a premating period that lasted less than 24 hr, and one female mated approximately six hours

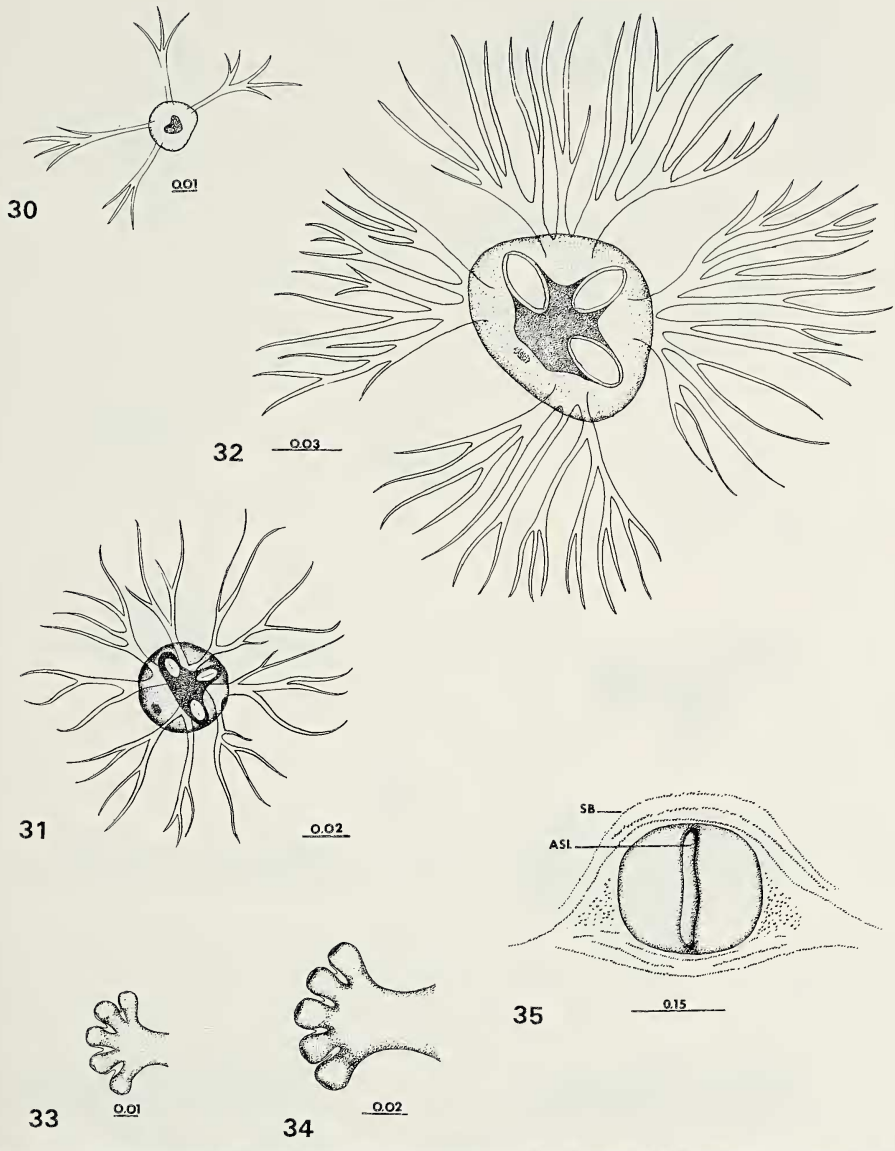


Fig. 30–35.—*Diplotoxa* sp. near *versicolor*. 30. Posterior spiracular plate, first instar. 31. Same, second instar. 32. Same, third instar. 33. Anterior spiracle, second instar. 34. Same, third instar. 35. Perianal pad, third instar.

after emerging. No overt courtship behavior was observed. Mating usually occurred during late afternoon. During coitus, the male positioned himself above the female at about a 45° angle to her body. The head was positioned directly above the anterior portion of her scutellum, the front tarsi rested slightly in front of the wing bases of the female, and the mid and hind tarsi clasped the sides of the female's abdomen. The wings of both sexes remained folded during mating which lasted from eight to over 30 minutes ($n$ = 12).

The preoviposition period from mating to the first deposition of eggs usually

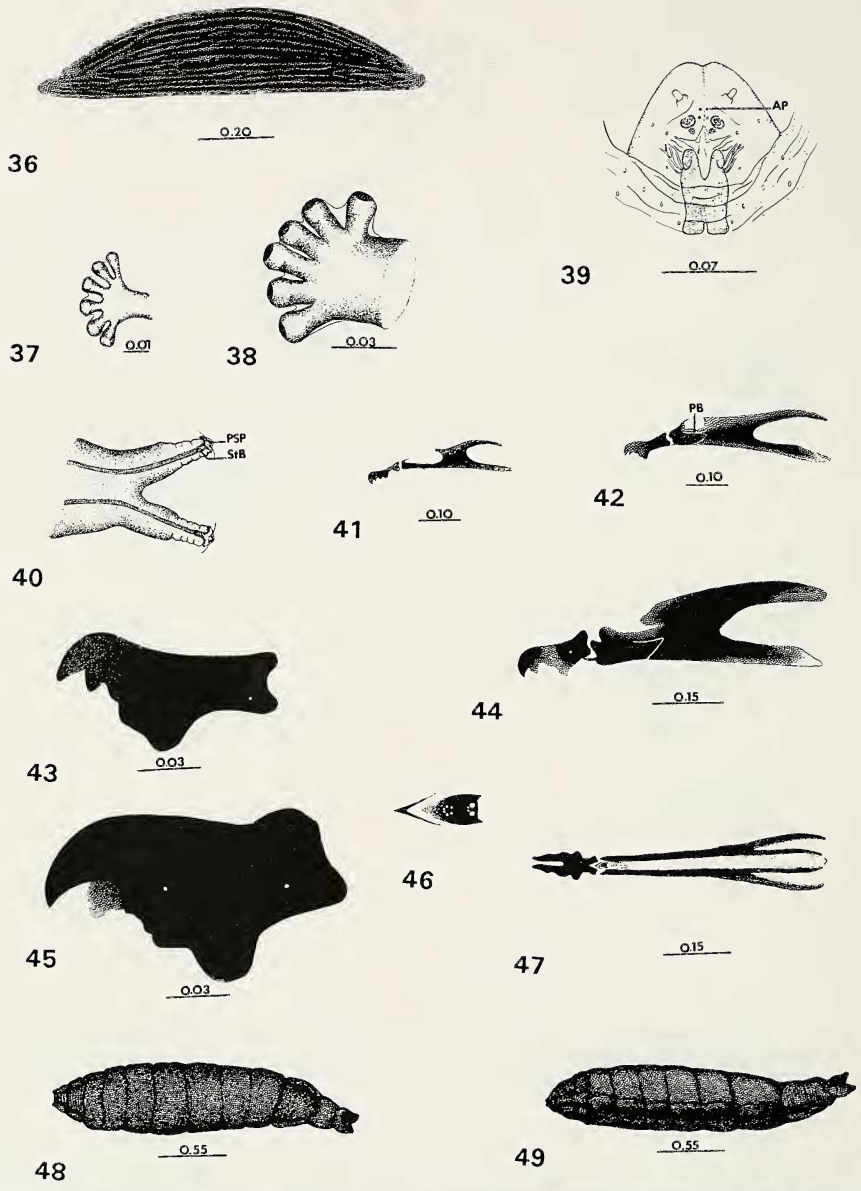


Fig. 36–49.—*Diplotoxa inclinata*. 36. Egg. 37. Anterior spiracle, second instar. 38. Same, third instar. 39. Ventral view of segment 1, third instar. 40. Dorsal view of stigmatic tubes, third instar. 41. Lateral view of cephalopharyngeal skeleton, first instar. 42. Same, second instar. 43. Mandible, second instar. 44. Lateral view of cephalopharyngeal skeleton, third instar. 45. Mandible, third instar. 46. Ventral view of subhypopharyngeal and ligulate sclerites, third instar. 47. Ventral view of cephalopharyngeal skeleton, third instar. 48. Puparium, dorsal view. 49. Same, lateral view.

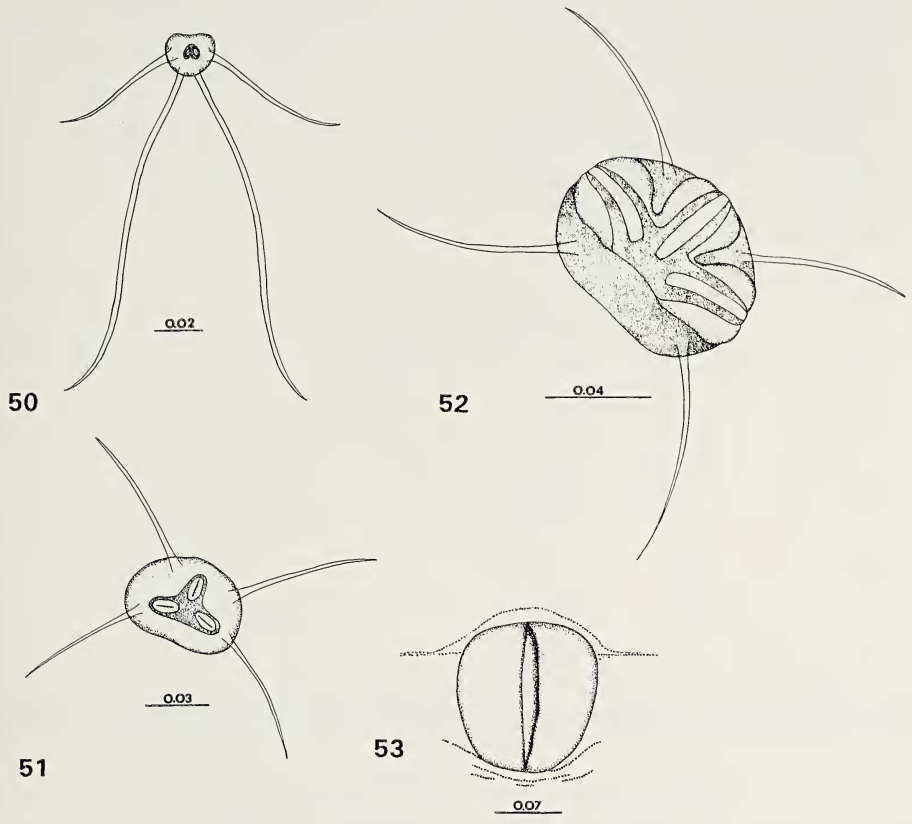


Fig. 50–53.—*Diplotoxa inclinata*. 50. Posterior spiracular plate, first instar. 51. Same, second instar. 52. Same, third instar. 53. Perianal pad, third instar.

was less than a day, and one female began ovipositing six hours after mating. If *Eleocharis* stems were not available, females delayed oviposition for over a week then laid a few eggs on the peat moss that formed a moist substrate in the breeding jars. These females died a day or so after oviposition. In contrast, females confined with *Eleocharis* readily oviposited on the stems and lived for several days after ovipositing. Five females laid 86, 89, 72, 62, and 86 eggs, respectively ($\bar{x} = 79$), over a 16-day period. Usually 4–5 eggs were laid by a female each day once oviposition began. Most of the eggs were deposited at the base of a stem just above the level of the peat moss substrate. A few eggs were placed higher on the stems, but none was placed on the inflorescence. The incubation period lasted 4–5 days ($n = 25$).

In nature, eggs were attached to stems just above the water level and oriented parallel to the stem. One or two eggs were usually found on each stem, although a few stems supported as many as five eggs. Stems occurring in deeper water were more heavily infested than those in shoreline situations.

Newly-hatched larvae crawled down the stem and entered young shoots at the base of the plant where they fed as primary invaders. Following the first larval molt, larvae ate their way downward to the bases of the shoots and penetrated into the rhizomes attached to the crown. Here, they fed on succulent meristematic

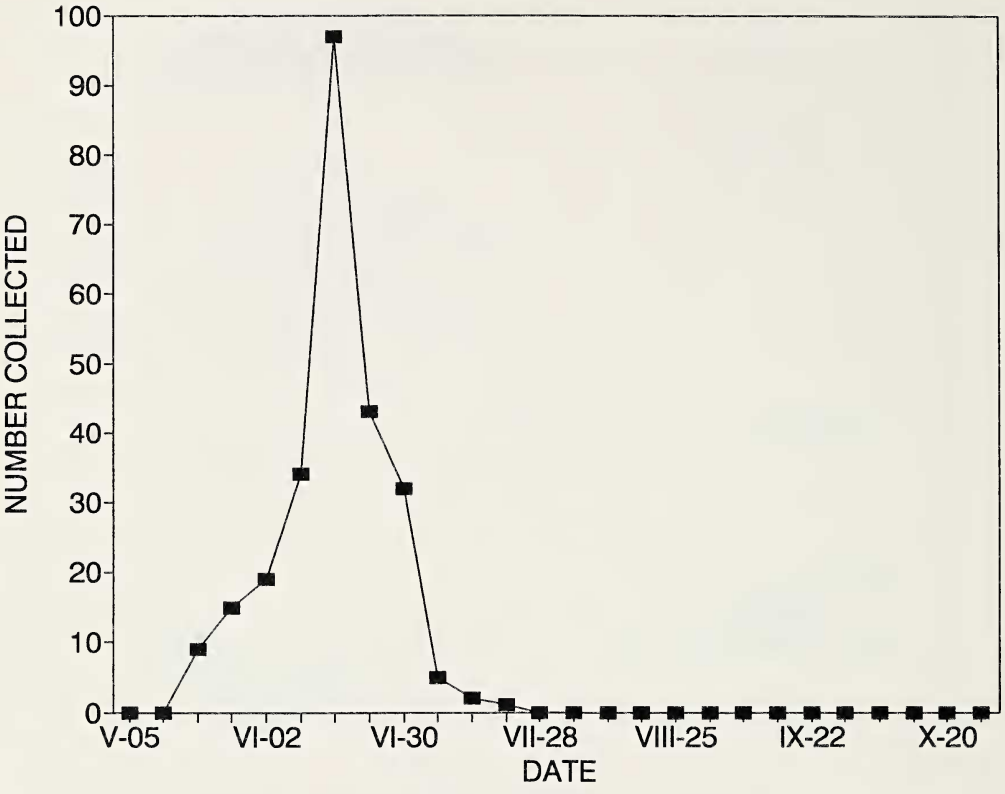


Fig. 54.—Seasonal distribution of *Chlorops obscuricornis.*

tissues, leaving a distinct feeding trail through the rhizome. When a larva reached a tiller arising from the rhizome, it entered the upright shoot and consumed its contents. It then returned to the rhizome and fed along it until another tiller was encountered. This process was repeated several times, and the larva usually was fully grown by the time it reached the tip of the rhizome. Pupation occurred within the feeding trail near the distal end of a rhizome. Shortly before forming a puparium, the larva inserted its posterior spiracles into the living tissue adjacent to the feeding trail.

In the laboratory, newly-hatched larvae were placed on the tip of a rhizome, the succulent tissue of which was surrounded by a protective sheath. Larvae quickly removed under the sheath and began to feed on the meristem. However, duration of larval stadia under laboratory conditions could not be determined. Collections of larvae and puparia in nature allowed for estimations of the third larval and pupal stadia. The third stadium lasted 5–6 days ($n$ = 12); the prepupal period, 30–48 hr ($n$ = 5); and the pupal period, 10–13 days ($n$ = 4).

Overwintering occurred as second instars in quiescence, feeding recommenced in April, and pupation occurred in the last two weeks of April.

The third instars and pupae of this species were easily distinguished from those of the other species of *Diplotoxa* by their greenish color.

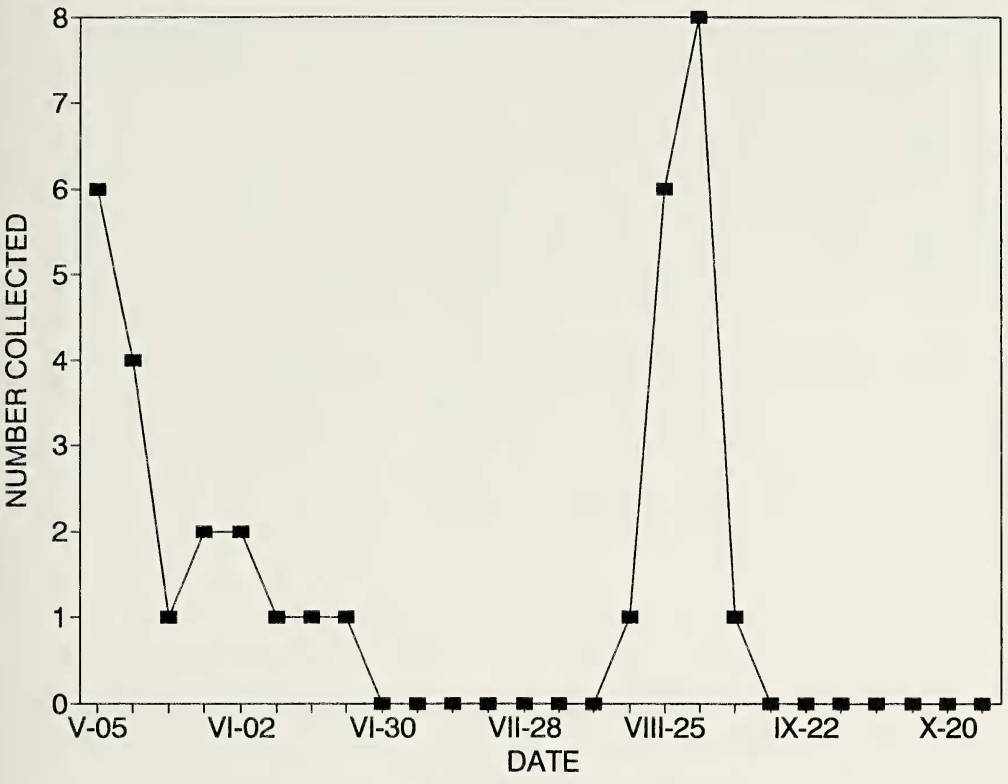


Fig. 55.—Seasonal distribution of *Diplotoxa inclinata.*

## *Diplotoxa nigripes* (Coquillett)

*Diplotoxa nigripes* ranges from South Dakota and Kansas east to Québec, Maine, and the District of Columbia (Sabrosky, 1965). It was, by far, the most abundant of the three species of *Diplotoxa* collected in Ohio.

Adults were abundant between June 13 and October 3 in strands of *Eleocharis obtusa,* but were only occasionally collected in stands of *E. smallii.* No adults were obtained in the sweep samples taken weekly in a stand of *E. smallii* growing in a roadside ditch, nor in weekly net samples from reed canary grass (*Phalaris arundinacea* L.) and two species of sedges (*Carex lacustris* Willd., *C. stricta* Lam.) in a freshwater marsh near Kent during the warm seasons of 1984 (Todd and Foote, 1987) and 1989. The larval rearings as well as the adult collections indicate that the primary host of this species is *E. obtusa.*

Adults usually rested on the stems of the host plant facing downward. Field-collected males lived 14–37 days in the laboratory ($n = 4$); females, 7–45 days ($n = 8$). In contrast, females reared in the laboratory rarely lived more than 30 days. Mating was observed three times in nature on stems of the host plant during late afternoon. No overt courtship behavior was observed. During copulation, the male was positioned above the female and facing in the same direction with his head at about the level of her scutellum. The wings of both sexes remained folded during mating. The male's fore tarsi rested on the bases of the female's wing, and

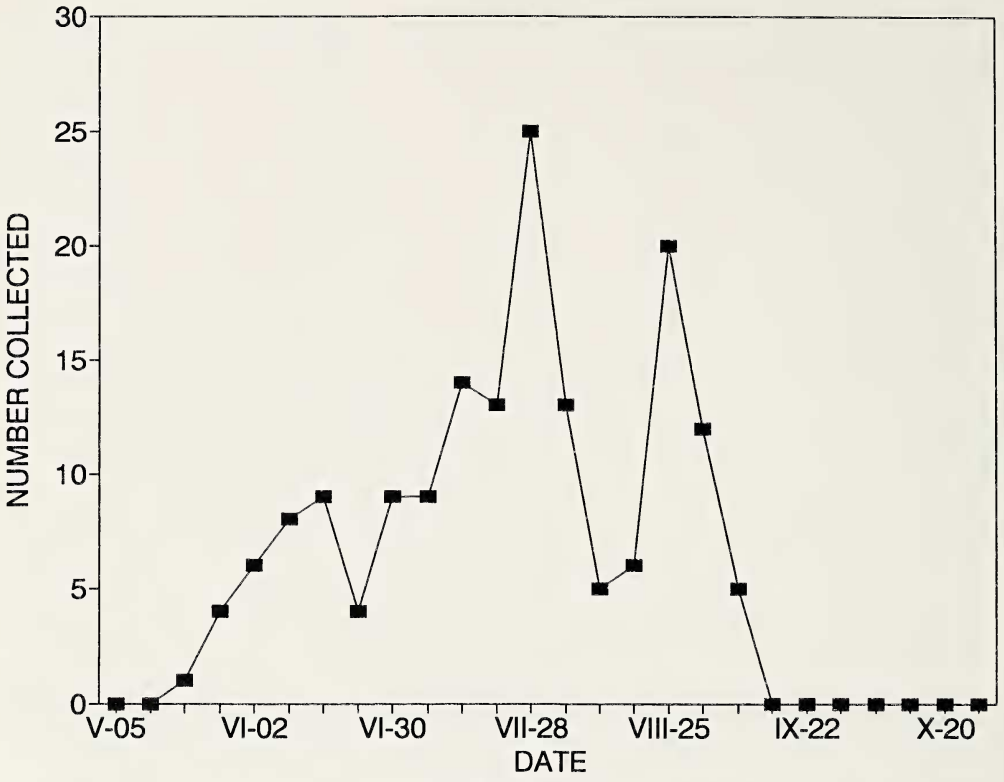


Fig. 56.—Seasonal distribution of *Diplotoxa* sp. near *versicolor.*

the middle and hind tarsi were pressed against the sides of her abdomen. Mating lasted an average of ten minutes ($n$ = 3). Males terminated mating by moving anteriorly off the body of the female.

Field-collected females laid numerous eggs in the laboratory breeding jars, although no reared females oviposited. Three females held in the laboratory for 11 days laid 56, 61, and 64 eggs, respectively. Laboratory-held females showed no particular preference for any part of the host plant, although more eggs were deposited on inflorescences and near the base of the stem. In contrast, host plants collected in nature never had eggs anywhere except on the stem bases. Eggs were not inserted into the stem tissue, but were affixed to the upper end of the reddish brown sheath that encircled the lower six inches of the stem. Only one or two eggs were found on each stem.

The incubation period lasted 5–7 days under laboratory conditions, although more than 80% of the eggs laid after the first week of October failed to hatch. The incubation period of those few October-laid eggs that did hatch was considerably extended, lasting 13–15 days. These observations suggest that autumn-deposited eggs enter diapause and overwinter.

The larval stages were very difficult to rear in the laboratory because they would not stay in stems of the host plant once decay commenced, a process that usually began less than a day after the plant was removed from nature. They fed as primary invaders within young shoots, leaving a distinct feeding trail of decaying tissue

as they progressed. Each larva usually attacked at least two shoots, although occasionally as many as five were damaged. Usually only one third instar was found in each plant, although two or more larvae may have initially invaded the plant.

Fully-grown larvae retreated to the base of the shoot in which they had fed and ate a hole into the rhizome to which the shoot was attached. They then reversed position and inserted their relatively long spiracular tubes into the cavity created in the rhizome. This behavior probably ensured an adequate oxygen supply for the developing pupa. The prepupal period from formation of the puparium to appearance of the contained pupa lasted four days; the pupal period, 19–25 days ($n = 5$).

With an incubation period of 5–7 days, a larval period of ca 30 days, a prepupal and pupal period of 23–29 days, and a preoviposition period of at least two or three days, a life cycle was completed in about two months. Overwintering occurred as eggs or as newly-hatched larvae within shoots of the host plant. Larval development accelerated in April, and larvae became fully grown in mid- to late May. Pupation then ensued, and adults emerged during June. Adult numbers increased again in late August, suggesting that two generations a year are produced in northern Ohio.

*Diplotaxa* sp. near *versicolor* (Loew)

This sibling species of *D. versicolor* was common in northeastern Ohio in freshwater marshes containing its host plants, *Eleocharis obtusa* and *E. smallii.* Numerous adults of *D. versicolor* were swept from a small (3 × 1 m) stand of the path rush, *Juncus tenuis* Willd. (Juncaceae), but were not encountered in stands of *Eleocharis,* suggesting that the two species are trophically separated.

The earliest seasonal record for adults in northeastern Ohio was May 19; the latest, October 8 (Fig. 56). Field-collected females lived 15–47 days in the laboratory ($n = 5$); males, 9–40 days ($n = 7$). Mating behavior and copulation position resembled that of *D. nigripes.*

Laboratory-reared females showed no preference for any particular species of *Eleocharis* and readily oviposited on both *E. obtusa* and *E. smallii* as well as on stems of the rush genus *Juncus.* However, eggs were found only on stems of *E. obtusa* in nature, usually 2.5–5.0 cm above the crown. The incubation period lasted 4–6 days ($n = 15$).

Newly-hatched larvae that were placed near the tips of young shoots of *Eleocharis* quickly crawled down the stem until they encountered the leaf sheath that surrounded the lower half of the stem. They then moved under the edge of the sheath and continued their downward movement to the crown. At the base of the shoot each larva paused and broke into the stem, subsequently feeding as stem borers. Usually only one or two larvae, occasionally three, were found in any one shoot.

Apparently there was only one generation a year in northern Ohio (Fig. 56). Larvae that had fed heavily on young shoots during the summer months remained in the plant tissues as second instars through the ensuing winter. However, overwintering larvae did not appear to be in diapause, as they quickly resumed feeding when brought into the laboratory. Feeding larvae formed a distinct linear trail of browned, decaying tissues as they moved along the length of the shoot.

Fully grown larvae were found near the bases of shoots during late March and early April. Before forming puparia in late April, larvae moved to the base of the

shoots at the crown. Prior to pupating, larvae formed a small cavity in the firm tissue occurring where the shoots united with the roots. The larvae then reversed direction and placed their posterior spiracular tubes in the cavity similar to the behavior observed in *D. nigripes*. The pupal period for the single pupa that produced an adult was 21 days.

Fifteen of the 16 field-collected puparia produced parasitic wasps belonging to an undetermined species of *Chaenusa* (Braconidae).

## Key to Third-instar Larvae

1. Posterior spiracles at tips of short stigmatic tubes; spiracular plates lacking spiracular hairs ..... *C. obscuricornis*
   Posterior spiracles at tips of very elongate stigmatic tubes (Fig. 3); spiracular plates with spiracular hairs (Fig. 52) ..... 2
2. Spiracular plates appearing trilobed, with unbranched spiracular hairs (Fig. 52); tentoropharyngeal and hypopharyngeal sclerites separate (Fig. 44); living larva usually greenish ..... *D. inclinata*
   Spiracular plates unlobed, with dichotomously branched spiracular hairs (Fig. 32); tentoropharyngeal and hypopharyngeal sclerites partially fused; body of living larva white ..... 3
3. Each spiracular hair with 5–7 branches (Fig. 15) ..... *D. nigripes*
   Each spiracular hair with ten or more branches (Fig. 32) ..... *D.* sp. nr. *versicolor*

## Descriptions of Immature Stages

### *Diplotoxa inclinata*

*Egg.*—(Fig. 36) length 1.0–1.10 mm, greatest width 0.20–0.25 mm. White, elongate, tapered. Ventral surface very flat, transparent, unridged. Chorion finely striated, with numerous ridges forming a complex pattern. Micropylar end larger than posterior end, both ends smooth and nonstriated.

*First-instar Larva.*—Similar to third-instar larva except in following characters. Length 1.00–2.80 mm, greatest width 0.20-0.31 mm. White, transparent. Intersegmental constrictions conspicuous. Posterior spiracular plates (Fig. 50) circular, borne at end of elongated stigmatic tubes. Spiracular openings heavily sclerotized, probably two in number. Four unbranched, spiracular hairs, middle two twice as long as remaining two. Cephalopharyngeal skeleton (Fig. 41): length 0.30–0.41 mm; heavily pigmented, posterior portion of tentoropharyngeal cornua hyaline; hypopharyngeal and tentoropharyngeal sclerites fused; no parastomal bars; thin sclerotized wing projecting dorsoposteriorly from hypopharyngeal sclerite; mandibles with two accessory teeth.

*Second-instar Larva.*—Similar to third-instar larva except in following characters. Length 3.50–4.70 mm, greatest width 0.40–0.60 mm. Posterior spiracular plate (Fig. 51) circular with three heavily sclerotized and indistinct spiracular openings. Four unbranched spiracular hairs, all hairs equal in length. Stigmatic scar and spiracular trabeculae, indistinct. Anterior spiracles (Fig. 37) enclosed in transparent, ensheathing membrane; spiracles creamy white, fan-shaped, with six marginal papillae. Cephalopharyngeal skeleton (Fig. 42) more pigmented than that of first instar. Posterior third of ventral cornua not pigmented. Hypopharyngeal and tentoropharyngeal sclerites almost entirely fused, leaving only faint tract of fusion line between sclerites. Indication of fusion between parastomal bar

and hypopharyngeal sclerites. Remnant of sclerotized wing extending dorsoposteriorly from anterior ridge of hypopharyngeal sclerite, mandibles (Fig. 43) fused dorsally, strongly pigmented except for apical and accessory teeth. One large apical tooth, one and possibly two smaller accessory teeth. Only one window visible.

*Third-instar Larva.*—Length 5.60–7.50 mm, greatest width 0.60–0.85 mm. Similar to third-instar larva of *D. nigripes* except for following characters. First segment (Fig. 39) bilobed apically, each lobe bearing one short, fleshy two-segmented antenna and one maxillary palp with slightly sclerotized C-shaped ring basally and containing 11–13 papillae. Each lobe also bearing eight sensory papillae, one dorsal and one frontal papilla, three submaxillary papillae (two anterior and one posterior), two lateral papillae, and one genal papilla. Genal rami leading into mouth cavity. Facial mask with numerous, large, posteriorly pointed, V-shaped spinules. Segments 2 and 3 with 10–15 irregular rows of fine spinules, only 5–10 of these rows completely encircling segment. Segments 4–11 with 15–25 overlapping, irregular rows of large, blunt spinules, only 10–15 of these rows continue around segment. Perianal pad (Fig. 53) level with ventral surface; surrounded anteriorly by compact rim of unequal-sized, irregularly-spaced, round spinules and ventrally by three distinct rows of small rounded spinules.

Anterior spiracles (Fig. 38) large and conspicuous, creamy white, extending perpendicularly from body, fan-shaped, with six finger-like marginal papillae, each papilla enclosed within ensheathing membrane. Stigmatic tubes (Fig. 40) elongate, constricted. Posterior spiracular plates (Fig. 52) posterodorsally at apices of stigmatic tubes. Spiracular bulb and spiracular trunk creamy white, large, conspicuous, and trifurcating into three large lobed structures (Fig. 40), each lobe possessing dorsal spiracular opening. Spiracular trunk heavily pigmented, spiracular openings indistinct, appearing as continuous, dark, trilobed structure. Stigmatic scar somewhat circular, not conspicuous. Four unbranched spiracular hairs. Trabeculae indistinguishable.

Cephalopharyngeal skeleton (Fig. 44) length 0.64–0.78 mm. Heavily sclerotized except for posterior ends of dorsal and ventral cornua. Hypopharyngeal and tentoropharyngeal sclerites separate. Parastomal bars present, fused anteriorly to dorsal surface of hypopharyngeal sclerite. Hypopharyngeal slcerite H-shaped in ventral view (Fig. 47). Dorsal cornua of tentoropharyngeal sclerite not joined by bridge; floor of tentoropharyngeal sclerite faintly pigmented. Mandibles (Fig. 45) heavily pigmented except for accessory tooth, fused dorsally, two circular windows, accessory tooth with protrusion anteriorly.

### *Diplotoxa nigripes*

*Egg.*—(Fig. 10) length 1.15–1.80 mm, greatest width 0.20–0.25 mm. White. Elongate, with micropylar end only slightly larger than posterior end, micropyle turned upward. Ventral surface somewhat flat, opaque with one or two faint ridges. Chorion with 11–12 large, prominent reticulations; micropylar and opposite end without reticulations. Eggs with 4–5 diverging reticulations, one diverging towards posterior end on dorsal surface, remainder on lateral surface.

*First-instar Larva.*—Similar to third instar except in following characters. Length 1.20–2.18 mm, greatest width 0.20–0.43 mm. White, integument transparent. Posterior spiracular plates (Fig. 13) borne at distal end of elongated stigmatic tubes. Spiracular tubes pigmented, spiracular openings indistinct, but probably two in number, radiating out from stigmatic scar. Four spiracular hairs, each with one main trunk bifurcating at distal end. Metapneustic. Cephalopharyngeal skel-

eton (Fig. 4) pigmented except on posterior portion of ventral cornua and tip of dorsal cornua, length 0.35–0.50 mm. Hypopharyngeal and tentoropharyngeal sclerites fused, no parastomal bars. Thin sclerotized wing projecting dorsoposteriorly from dorsoanterior ridge of hypopharyngeal sclerite. Mandibles of one sclerite, one accessory tooth.

*Second-instar Larva.*—Similar to third instar except in following characters. Length 2.40–3.81 mm, greatest width 0.55–0.68 mm. Posterior spiracular plate (Fig. 14) circular to oval, three sclerotized and indistinct spiracular openings appearing as dark, trilobed structure. Four branched spiracular hairs. Stigmatic scar not distinct. Trabeculae indistinct. Anterior spiracles (Fig. 16) creamy white, fan-shaped, with seven marginal papillae. Transparent membrane enclosing papillae. Cephalopharyngeal skeleton (Fig. 6) pigmented except on posterior end of ventral cornua. Length 0.58–0.68 mm. Hypopharyngeal and tentoropharyngeal sclerites showing fusion line. Most of each parastomal bar fused with dorsal surface of hypopharyngeal sclerite. Anterior end of bar forming knob-like protuberance anterodorsally from hypopharyngeal sclerite. Mandibles (Fig. 8) well-pigmented except for apical and accessory teeth, one sclerite; one large apical tooth and two accessory teeth. Subhypostomal and ligulate sclerites semitransparent.

*Third-instar Larva.*—(Fig. 1) length 5.50–6.70 mm, greatest width 0.85–1.00 mm. Creamy white, integument transparent to translucent. Body elongate, cylindrical, tapering anteriorly from third thoracic segment. Posterior end tapering and terminating in two elongated stigmatic tubes. Body of stigmatic tube (Fig. 3) thick, integument extending beyond body, terminating in spiracular plates. First segment (Fig. 2) bilobed apically, each lobe bearing short, two-segmented antenna, two maxillary palps, each palp with slightly sclerotized basal C-shaped ring, six maxillary papillae; six sensory papillae including one prefrontal, three frontal (two anterior, one posterior), one or two lateral, one genal papillae. Genal rami thin, not bifurcating, directed toward oral opening. Facial mask with numerous rows of spinules that completely encircle larva.

Spinule bands with 20–30 short, irregular rows of spinules at anterior end of all thoracic and abdominal segments. Spinules in abdominal segments reduced and indistinct, forming a fine, linear fold. Spinule bands more numerous on ventral surface, only 10–15 rows continuing around segment.

Anterior spiracles (Fig. 17) large, conspicuous, perpendicular to body. Creamy white, fan-shaped with seven finger-like marginal papillae, ensheathing membrane extending closely over papillae.

Posterior spiracular plates (Fig. 15) circular, located distally on stigmatic tubes. Spiracular bulb and spiracular trunk not conspicuously enlarged or trifurcating (Fig. 3). Three spiracular openings not distinct, appear as continuous, dark, trilobed structure. Stigmatic scar present but not conspicuous. Four spiracular hairs, each immediately bifurcating into two main branches and many secondary branches. Trabeculae approximately 18 per spiracular opening.

Cephalopharyngeal skeleton (Fig. 7) length 0.88–0.95 mm. Heavily sclerotized except transparent posterior ends of dorsal and ventral cornua. Hypopharyngeal and tentoropharyngeal sclerites not completely fused. Parastomal bar fused with dorsal surface of hypopharyngeal sclerite, anterior end of parastomal bar extending anterodorsally from hypopharyngeal sclerite. Dorsal cornua not joined by bridge, floor of tentoropharyngeal sclerite lightly pigmented. Floor of hypopharyngeal sclerite (Fig. 5) wide, lightly sclerotized, H-shaped when viewed ventrally. Mandibles (Fig. 9) heavily pigmented except for accessory tooth, one posterior window.

Not connected dorsally, large apical tooth, one blunt accessory tooth. Subhypostomal sclerite beneath anterior edge of hypopharyngeal sclerite, with two large circular windows, slightly visible when viewed internally. Ligulate sclerite semitransparent, V-shaped, anterior to subhypostomal sclerite, anvil shaped when viewed laterally.

*Puparium.*—(Fig. 11, 12) length 5.10 mm, greatest width 1.50 mm. Mostly light golden-brown, dark brown to black anteriorly, stigmatic tubes black. Cuticle very thin and transparent, developing pupa clearly visible. Elongated anterior and posterior ends dorsoventrally flattened to form distinct lateral ridges on segments 1–4 and 9–11. Stigmatic tubes large, heavily sclerotized, extending in various positions. Anterior spiracles poorly developed, located anteriorly on dorsal cephalic cap, fan-shaped and silver-white, with seven marginal papillae. Posterior spiracular plate rounded, spiracular openings indistinct. Perianal pad depressed. Puparium retaining spinule bands of third-instar larva.

*Diplotoxa* sp. near *versicolor*

*Egg.*—(Fig. 29) length 0.80–1.00 mm, greatest width 0.12–0.15 mm. White, elongate, and tapered. Ventral surface somewhat flattened, transparent and unridged. Chorion striated, with ridges diverging and converging especially at ends and on the dorsal surface. Micropylar end larger than posterior end, both ends smooth and nonstriated.

*First-instar Larva.*—Similar to third instar except in following characters. Length 0.90–2.20 mm, greatest width 0.15–0.21 mm. White, integument transparent. Posterior spiracular plates (Fig. 30) at ends of elongated stigmatic tubes. Spiracular trunks deeply pigmented. Spiracular openings not distinguishable, probably two in number positioned to form dark, heart-shaped structure. Four spiracular hairs, each with single long trunk terminating in either three or four shorter branches. Larva metapneustic. Cephalopharyngeal skeleton (Fig. 24) length 0.25–0.35 mm, pigmented except for hyaline posterior portion of ventral cornua and tip of dorsal cornua. Hypopharyngeal and tentoropharyngeal sclerites fused, parastomal bars lacking. Thin, sclerotized wing projecting dorsoposteriorly from dorsoanterior ridge of hypopharyngeal sclerite. Mandibles with one accessory tooth.

*Second-instar Larva.*—Similar to the third instar except in following characters. Length 3.20–4.00 mm, maximum width 0.45–0.60 mm. Posterior spiracular plate (Fig. 31), circular to oval, three indistinct spiracular openings on brown, trilobed structure. Four, multibranched spiracular hairs, each with short trunk that forks into two main branches that each terminate in 2–6 shorter branches. Stigmatic scar and trabeculae indistinct. Anterior spiracles (Fig. 33) creamy white, fan-shaped, with five marginal papillae; with transparent ensheathing membrane around papillae. Cephalopharyngeal skeleton (Fig. 25) more pigmented than in first instar. Posterior ends of ventral cornua not pigmented. Hypopharyngeal and tentoropharyngeal sclerites almost entirely fused. No dorsal wing extending from hypopharyngeal sclerite. Parastomal bars fused to hypostomal sclerite except for anterior end which appears as thick, anterodorsal protuberance. Mandibles well-pigmented except for apical and accessory teeth; one large apical tooth and two accessory teeth; 4–6 circular windows. Subhypostomal and ligulate sclerites poorly pigmented.

*Third-instar Larva.*—(Fig. 18, 19) similar to third-instar larva of *D. nigripes* except in following characters. Length 4.50–5.50 mm, maximum width 0.70–0.95 mm. Maxillary palp of segment 1 (Fig. 20) with 7–11 papillae. Facial mask with

numerous large, V-shaped spinules. Segment 1 with 20–25 compact, short, irregular rows of spinules at anterior end, spinule rows completely encircling segment. Segments 2 and 3 with 15–20 thick, irregular rows of large, blunt spinules that encircle anterior end of each segment. Spinule bands dark due to slight sclerotization or impregnation by dirt. Segments 4–8-with 15–20 short, irregular rows of V-shaped spinules encircling segments. Spinule bands on dorsal surface more linear, fine, and composed of smaller spinules. Ventral surface of segments 9 and 10 containing approximately 20–30 short, irregular, fine rows of spinules, only 7–15 rows encircling segments. Segment 11 with reduced spinule bands, individual spinules indistinct, forming fine lines, no spinule bands on dorsal surface. Perianal pad (Fig. 35) with three fine rows of spinules anteriorly and 3–5 rows posteriorly, cluster of irregularly spaced large, U-shaped spinules between anterior and posterior rows.

Anterior spiracles (Fig. 34) large, conspicuous, creamy white, extending perpendicularly from body, fan-shaped, with five finger-like marginal papillae, each papilla enclosed within ensheathing membrane. Stigmatic tubes elongate. Posterior spiracular plates (Fig. 32) posterodorsally at end of stigmatic tubes. Stigmatic bulbs and spiracular trunks normal. Spiracular trunks heavily pigmented, spiracular openings indistinct, appearing as continuous, dark, trilobed structure. Stigmatic scar somewhat ovoid. Four, multibranched spiracular hairs, each with main trunk diverging into three or four branches that terminate in many smaller branches. Trabeculae indistinguishable.

Cephalopharyngeal skeleton (Fig. 26) length 0.70–0.90 mm, greatest width 0.15 mm. Heavily sclerotized except for posterior end of ventral cornua. Hypopharyngeal and tentoropharyngeal sclerites partially fused. Parastomal bars fused with dorsal surface of hypopharyngeal sclerite, anterior end of parastomal bar extending out anterodorsally from hypopharyngeal sclerite. Hypopharyngeal sclerite H-shaped when viewed ventrally (Fig. 21). Floor of tentoropharyngeal sclerite (Fig. 21) lightly pigmented except for transparent posterior end, dorsal cornua not joined by bridge. Mandibles (Fig. 23) heavily pigmented except for accessory tooth, one circular window. Subhypostomal sclerite beneath anterior edge of hypopharyngeal sclerite, somewhat heart-shaped. Slightly visible when viewed laterally, ligulate sclerite V-shaped, elongate, anterior of subhypostomal sclerite, semitransparent. No dentate sclerites.

*Puparium.*—(Fig. 27, 28) similar to puparium of *D. nigripes* except in following characters. Length 2.80–3.30 mm, greatest width 0.75–0.90 mm. Gold to reddish brown, dark brown cephalic cap. Cuticle slightly transparent. Anterior spiracles poorly developed, anterior on dorsal cephalic cap, fan-shaped with five marginal papillae. Spinule bands appearing ridge-like, completely encircling segments, becoming coarse and deeply grooved at anterior and posterior ends of puparium. Intersegmental constrictions distinct. Segment 1 partially invaginated. Posterior stigmatic tubes flattened dorsoventrally, deeply pigmented posteriorly. Spiracular plates black, oblong, spiracular openings not visible. Anal slit distinct, slightly depressed.

## Discussion

This study suggests that the larval stages of many, if not all, species of the genus *Diplotoxa* are associated with spike-rushes of the genus *Eleocharis*. Adults of seven species were collected in Ohio or Montana from stands of *Eleocharis* (Wearsch, 1968), eggs of at least five species were discovered on *Eleocharis* stems, and larvae of four species were found feeding in stems or rhizomes.

*Eleocharis* plants are infrequently attacked by other insect larvae except for a few species of Lepidoptera and Coleoptera. *Eleocharis* species grow in marshy areas, along with other sedges and rushes, frequently form extensive pure stands, and are relatively undisturbed by human activity. The many sprouts, which are continually produced at the base of the plant during the warm season, and the thick, branched rhizome system offer very succulent food sources. Meristematic tissue in monocots such as *Eleocharis* is basal in position within the stem, and typically has a higher energy content than nonmeristematic tissue (Hirose et al., 1989), which explains the concentration of feeding by chloropid larvae at the base of the stem or in rhizomes.

Primary invaders (larvae feed on living plant tissue) of *Eleocharis* stems are best represented by *C. obscuricornis, D.* sp. near *versicolor,* and *D. nigripes.* In contrast, the morphology of the larvae of *D. inclinata* includes some features of a secondary invader (larva feeds on tissue damaged by a primary invader) and some of a primary invader. A comparison of the cephalopharyngeal skeleton of various species of primary and secondary invaders in the family Chloropidae indicates that secondary invaders possess separate tentoropharyngeal and hypopharyngeal sclerites, whereas these sclerites are fused in primary invaders.

Although the overall appearance of chloropid larvae is similar, species are distinguishable in size, color, and appearance of the stigmatic tubes and spiracular hairs. *Chlorops* larvae differ from those of *Diplotoxa* in having spiracular openings at the distal ends of sclerotized extensions that protrude from short stigmatic tubes, and in lacking spiracular hairs. In contrast, larvae of *Diplotoxa* possess very elongate stigmatic tubes and have long spiracular hairs.

Identifying species of *Diplotoxa* from preserved larval specimens is difficult, although living larvae of *D. inclinata* are easily distinguished from those of the other species we studied by their greenish color. The bulb and internal stigmatic chamber of the stigmatic tubes of this species are enlarged, have a dark creamy color, and branch into three prominent lobes. The spiracular plate possesses a trilobed structure bearing the spiracular slits and has only four nonbranching spiracular hairs. *Diplotoxa* sp. near *versicolor* and *D. nigripes* have semitransparent internal stigmatic chambers, with the spiracular slits opening onto the flat spiracular plate. Both have a complex network of spiracular hairs.

The anterior spiracles of all three species of *Diplotoxa* consist of a fan-shaped structure with apical papillae. The number of papillae is relatively constant and distinctive for each species. *Diplotoxa* sp. near *versicolor,* the smallest of the three species, possesses five papillae; *D. inclinata,* the next largest, has six; and *D. nigripes,* the largest, has seven.

The cephalopharyngeal skeletons of *D.* sp. near *versicolor* and *D. nigripes* differ in only a few structures, whereas both differ markedly from that of *D. inclinata.* The skeletons of the first-instar larvae of *D. nigripes* and *D.* sp. near *versicolor* are almost identical, having a wing projecting from the anterior end of the hypopharyngeal sclerite, but the skeleton of *D. nigripes* is much larger. In the second instar of both species the wing of the hypopharyngeal sclerite is reduced or absent, and a knob-like structure is present. This knob probably is the anterior portion of the parastomal bar, the remainder of which has fused with the dorsal surface of the hypopharyngeal sclerite. The hypopharyngeal and tentoropharyngeal sclerites are not completely fused in the third instars of both species, suggesting that larvae of these species originally fed as secondary invaders of damaged stems. Fusion of these two sclerites probably gives greater support and rigidity to the cephalopharyngeal skeleton.

*Diplotoxa inclinata* apparently became a primary invader very recently, as the tentoropharyngeal and hypopharyngeal sclerites in the third instar are still separate. However, the cephalopharyngeal skeleton of the first instar resembles that of *D.* sp. near *versicolor* and *D. nigripes.* The projecting wing of the hypostomal sclerite is reduced in the second instar, and the parastomal bar, although evident, has fused anteriorly with the base of the projecting wing of the hypopharyngeal sclerite. In the third instar, this fusion is more nearly complete but not to the degree seen in third instars of the other two species. The third instar of *D. inclinata* has the mandibles fused dorsally, which may give greater rigidity for feeding upon the hard tissues of the rhizome.

The shape of the posterior spiracles is helpful in distinguishing among larvae of the four species. Two spiracular openings occur in the first instar, and three in the second and third instars. The spiracles in *D. nigripes* and *D.* sp. near *versicolor* are similar, although *D. nigripes* is larger, and all three *Diplotoxa* species possess spiracular hairs. The first instar has four large hairs with one or two terminal branches. The hairs of the second instars are more complex: each hair has a main trunk that divides immediately into two large branches, each of which in turn divides two or more times. The third instar possesses a very fine network of four sets of spiracular hairs. The basal trunk of each hair radiates immediately into three or four main branches, each of which branches again to form a fine network. In *D. inclinata,* in contrast, the spiracular hairs of all three instars are reduced and unbranched. The first instar has two very long and two shorter hairs, whereas in the second and third instars the four hairs are equally long.

In *C. obscuricornis* the posterior spiracles are reduced, sclerotized structures with three spiracular slits but no spiracular hairs. Oldroyd (1964) reported that some stem-boring species of *Chlorops* have become so well-adapted to their environment that the posterior spiracles are vestigial. They absorb oxygen through the cuticle. Larvae of *C. obscuricornis* show a tendency toward reduction of the posterior spiracles.

Larvae of all four species, whether feeding on stems or rhizomes, inserted their stigmatic tubes into living tissue or air spaces before forming puparia. This probably is a mechanism for ensuring sufficient oxygen for pupal development. Under natural conditions, pupae in living plants developed normally and produced adults. When cut plants containing puparia were brought into the laboratory, the pupae died shortly after the plants began to decay. Pupae that were removed from stems and placed upon peat moss continued to develop and eventually produced adults.

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